A NEW SPECIES OF *PLECTROHYLA* (ANURA: HYLIDAE) FROM A PREMONTANE RAINFOREST IN NORTHERN HONDURAS

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Abstract.—A new species of *Plectrohyla, P. chrysopleura,* from moderate elevations in the Cordillera Nombre de Dios of northern Honduras is described and illustrated, as is its tadpole. Its combination of prominent golden yellow flashmarks, blunt prepollex, moderate size, vocal slits present in males, spatulate teeth, and weakly to moderately tuberculate dorsal surfaces easily distinguishes it from the other species of *Plectrohyla.* Several problems with a recent phylogenetic analysis of the genus *Plectrohyla* are noted and a phylogenetic reanalysis indicates that the new species is the one closest to the ancestral stock of the genus.

Field work in the Quebrada de Oro region of northern Honduras continues to uncover herpetological novelties. The first trip was in June, 1980, and since that time, we have described a new genus and five new species of anurans from this area in the central portion of the department of Atlántida (McCranie & Wilson 1986; McCranie, Savage, & Wilson 1989; McCranie, Wilson, & Williams 1989; Savage et al. 1988). Recently, a sixth new anuran described below was collected. Quebrada de Oro is a tributary of the Río Viejo, in turn a tributary of the Río Cangrejal, which flows into the Caribbean at La Ceiba, Honduras (see McCranie, Wilson, & Williams 1989, for a description of the area).

In May 1988, we collected specimens of a distinctive new species of the montane genus *Plectrohyla* at the Quebrada de Oro locality. Adults were found at elevations ranging from 930 to 990 m. McCranie and Eric Hedl, then a member of the United States Peace Corps stationed in Trujillo, Honduras, returned in 1989 and collected one adult at 990 m and two tadpoles at 1010 m.

Although this species probably occurs in suitable localities at higher elevations in the Río Viejo drainage, the known elevational range is near the lower limit for this genus. Duellman & Campbell (1992) indicated that the known elevational range for the other fifteen species of *Plectrohyla* is 615 to 3500 meters. Most species of *Plectrohyla* occur at intermediate elevations (1500–2700 m; sensu Stuart 1963), but a few, including the one described herein, range downward into moderate elevations (600–1500 m; sensu Stuart 1963). *Plectrohyla teuchestes* ranges downward to ca. 1000 m, *P. guatemalensis* and *P. hartwegi* to slightly less than 1000 m (we have collected *P. guatemalensis* as low as 990 m in the Sierra de Agalta above Catacamas in Honduras), and *P. matudai* and *P. quecchi* occur as low as 615–700 m.

The region of the "golden stream" (Quebrada de Oro) has been surprisingly productive of new taxa (others remain to be described). It is a figurative "gold mine" and once again has produced something "golden," the "golden-sided tree frog."

Methods

All measurements are in millimeters, made to the nearest tenth with dial calipers with the aid of a dissecting microscope. The

Fig. 1.   *Plectrohyla chrysopleura,* new species, male holotype (USNM 316547), SVL 63.8 mm.

dorsal ground colors were compared to the color swatches in Smithe (1975). Color numbers used below refer to that publication. Webbing formulas follow Savage & Heyer (1967) as modified by Myers & Duellman (1982). Subjective evaluations of tadpole jaw sheath configurations are patterned after Altig & Johnston (1986). The phylogenetic analysis was conducted using Swofford's (1991) software package PAUP (Phylogenetic Analysis Using Parsimony, version 3.0s) on a Macintosh Plus.

Plectrohyla chrysopleura, new species
Fig. 1

Holotype. — National Museum of Natural History (USNM) 316547, an adult male from along the Quebrada de Oro (15°38′N,

86°47′W), 970 m elev., tributary of the Río Viejo, south slope of Cerro Búfalo, Cordillera Nombre de Dios, Departamento de Atlántida, Honduras, collected 23 May 1988 by James R. McCranie and Larry David Wilson. Original number LDW 8907.

Paratypes. — USNM 316548, adult male, same data as for holotype, except elevation 930 m; USNM 316549–50, both adult males, same data as for holotype, except elevations unrecorded and collected 3 May, 1988 by Gustavo A. Cruz; USNM 316551, adult male, same data as for holotype, except elevation 990 m and collected 1 August 1989 by Eric Hedl and James R. McCranie.

Diagnosis. — A species of *Plectrohyla* distinguished from its congeners by the following combination of characteristics: moder-

ate size (56.6–65.6 mm snout-vent length); dorsum weakly to moderately tuberculate; vocal slits present; maxillary-premaxillary teeth spatulate; no vertical rostral keel; prepollex flat, elongate, terminally blunt; dorsum Smoke Gray (color 45) with a bronze sheen or Cinnamon (color 123A); prominent golden yellow flashmarks present on front and hind limbs, side of body, axilla, and groin (all flashmarks hidden when frog is at rest).

Description of holotype.—Adult male with snout-vent length (SVL) of 63.8; tibia length 37.7, 59.1 percent of SVL; foot length 31.0, 48.6 percent of SVL; head length 21.4, 33.5 percent of SVL; head width 23.0, 36.1 percent of SVL. Snout of moderate length, distance from anterior edge of orbit to tip of snout 8.6, 134.3 percent diameter of eye; snout truncate in dorsal aspect and in profile, lacking a vertical rostral keel; canthal ridge slightly thickened; loreal region slightly concave; lips moderately thickened, slightly flared. Nostrils protuberant, directed dorsolaterally, situated near tip of snout; internarial distance 4.9; internarial area slightly depressed near point of convergence of canthal ridges; top of head flat; interorbital distance 6.3, 27.4 percent of head width; diameter of eye 6.4; width of eyelid 4.9, 21.3 percent of head width. Moderately heavy dermal fold extending posteriorly from posterior edge of orbit, merging with body contour above point of insertion of arm, barely covering upper edge of tympanum, remainder of tympanum distinct; diameter of tympanum 3.3 mm, 51.6 percent of eye diameter.

Arms moderately robust, forearm slightly heavier than upper arm; distinct transverse fold on wrist. No axillary membrane. Fingers long, slender; length of fingers from shortest to longest, 1-2-4-3, fourth toe nearly as long as second; disc on third finger subequal in size to tympanum; webbing vestigial between first and second fingers, webbing formula II 2-3 III 2 1/2-2$^+$ IV; subarticular tubercles large, subconical; distal

tubercle on fourth finger normal; supernumerary tubercles in single rows on proximal segments of fingers; pollex flat, elongate, terminally blunt, spine not protruding through skin, lacking nuptial excrescences. Heels slightly overlapping when hindlimbs extended to right angles of body; no transverse dermal fold on heel; inner tarsal fold extending full length of tarsus; no outer tarsal fold; inner metatarsal tubercle ovoid, barely visible from above; no outer metatarsal tubercle. Toes long, slender; length of toes from shortest to longest, 1-2-5-3-4, fifth toe nearly as long as third; discs moderately large; subarticular tubercles moderately large, subconical; supernumerary tubercles small, low, in single row on proximal segment of each digit; toes about three-fourths webbed, webbing formula I 1$^+$-1 1/2 II 1$^+$-2 III 1$^+$-2 IV 2-1$^+$ V.

Vent opening directed posteroventrally at level of mid-thigh; anal sheath short, broad. Skin on dorsal surface, throat, and chest weakly tuberculate; skin on ventral surfaces of forearms moderately tuberculate; skin on belly, ventral surfaces of thighs, and below vent granular; skin on ventral surface of shanks smooth. Tongue nearly round; upper jaw shallowly notched medially; maxillary-premaxillary teeth spatulate; vomerine teeth 6-5, situated on small elliptical elevations between ovoid choanae; vocal slits present, extending from midlateral edge of tongue to angle of jaw; vocal sac single, median, subgular.

Color in life: dorsum of head, body, and limbs Smoke Gray (color 45) with a slight bronze sheen; tympanum pale coppery bronze; lips slightly paler than remainder of head; iris gold with black reticulations; prominent golden yellow flashmarks at axilla, side of chest, and underside of arm (all contiguous), similar but slightly darker flashmarks at groin, on anterior surface of thigh, underside of shank, upper surface of tarsus, and upper surface of foot (all flashmarks hidden when frog at rest); chin and chest gray with a golden sheen; belly gray

Table 1.—Variation in measurements (in millimeters) and proportions (percentages) in five male *Plectrohyla chrysopleura*. Character abbreviations are in brackets. Means are in parentheses following ranges.

Character	Measurements and proportions
Snout–vent length [SVL]	56.6–65.6 (62.1)
Tibia length [TL]	29.3–37.7 (34.1)
(TL/SVL)	46.6–59.2 (54.9)
Foot length [FL]	26.5–31.6 (29.3)
(FL/SVL)	45.5–48.6 (47.1)
Head length [HL]	20.0–21.7 (20.7)
(HL/SVL)	32.4–35.5 (35.1)
Head width [HW]	20.8–23.0 (21.8)
(HW/SVL)	33.5–37.1 (35.1)
Snout length [SL]	7.6–9.2 (8.3)
(SL/ED)	121.2–146.0 (133.1)
Eye diameter [ED]	5.8–6.6 (6.3)
Internarial distance	4.3–5.2 (4.8)
Interorbital distance [IOD]	5.9–7.2 (6.3)
(IOD/HW)	27.4–31.4 (28.8)
Eyelid width [EW]	4.9–5.4 (5.2)
(EW/HW)	21.3–25.7 (23.8)
Tympanum diameter [TD]	3.0–3.8 (3.4)
(TD/ED)	47.0–58.7 (53.1)

with yellowish cast, as is undersurface of thigh; posterior thigh surface golden yellow with dense olive green smudging; palms pale gray; soles gray.

Color in alcohol: dorsal surfaces grayish-brown; ventral surfaces pale gray; flashmarks dirty white.

Variation.—Measurements and proportions of all specimens are given in Table 1. Color and pattern of the paratypes are in essential agreement with that of the holotype, except that the dorsal surfaces of USNM 316551 were Cinnamon (color 123A) in life. Most paratypes are somewhat more tuberculate on the dorsal surfaces than is the holotype.

Description of tadpole.—One lot of two *Plectrohyla* tadpoles (USNM 316552) presumed to be of this species (no other *Plectrohyla* is known from the type locality nor is expected to occur there) is available. A tadpole (Fig. 2A) in stage 36 (Gosner 1960) may be described as follows: body length

16.8; tail length 27.8; total length 44.6; body slightly depressed, a little wider than high; snout semicircular in dorsal aspect, rounded in profile; eyes moderately small, widely separated, directed laterally; nostrils situated at a point slightly closer to eyes than tip of snout, directed anterolaterally; spiracle sinistral, directed posterodorsally, situated near midline, at a point about two-thirds distance from tip of snout to posterior end of body; vent tube moderately long, dextral; caudal musculature robust, extending nearly to tip of rounded tail; height of caudal musculature at midlength of tail greater than height of either dorsal or ventral fins; dorsal fin extending very narrowly onto posterior end of body.

Oral disc (Fig. 2B) large, ventral, completely bordered by two rows of moderately large marginal papillae (ca. 10/mm); single row of submarginal papillae surrounding A-1 and P-3 tooth rows, larger (ca. 7/mm) than marginal papillae; submarginal papillary row expanding to two-three rows lateral to jaw sheaths; oral disc not emarginated; keratinized jaw sheaths medium-sized, bearing short, pointed serrations; upper jaw sheath widely arched, with well-developed lateral processes; lower jaw sheath widely V-shaped; labial tooth rows ⅔ with second anterior row narrowly interrupted medially; anterior tooth rows subequal, long, extending to lateral portion of oral disc; posterior tooth rows subequal, noticeably shorter than anterior rows.

The second tadpole is in stage 26 and has a body length of 13.4, a tail length of 20.9, and a total length of 34.3. This specimen is very similar in morphological features to the larger tadpole described above.

Color in life of the larger tadpole was as follows: body brown; caudal musculature creamy-tan, boldly spotted with brown; caudal fins clear with brown spots. The smaller tadpole was similar, except that it lacked the bold markings on the caudal musculature and tail fins.
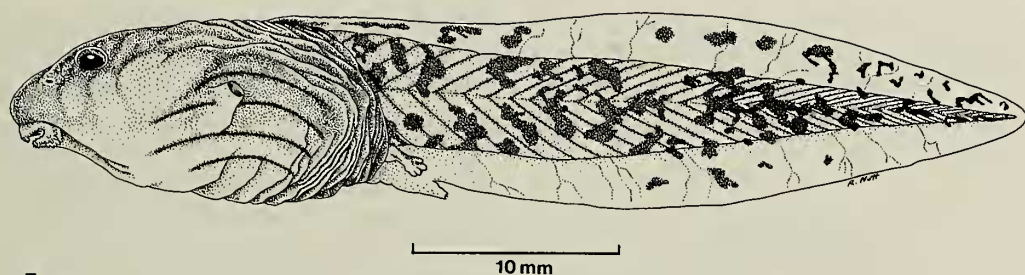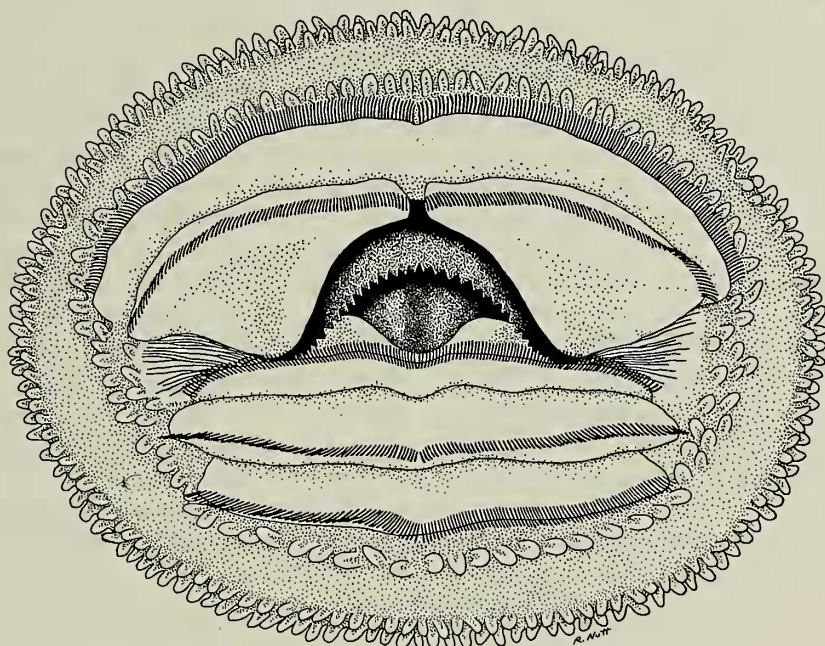
Natural history notes.—All adults, for

A

10 mm

B

1 mm

Fig. 2.   Tadpole of *Plectrohyla chrysopleura* (USNM 316552) in Gosner stage 36: (A) lateral view; (B) oral disc.

which information is available, were collected at night on boulders in splash zones near waterfalls in the Quebrada de Oro. The tadpoles were collected in a plunge pool in a small tributary of the Quebrada de Oro with tadpoles of *Ptychohyla spinipollex* and *Rana maculata.*

The vegetation of the Quebrada de Oro area lies in the Premontane Wet Forest formation of Holdridge (1967), and was described by McCranie, Wilson, & Williams (1989). The section of Quebrada de Oro in which we have worked since 1980 was decimated by a huge landslide in November of 1988, precipitated by deforestation on the steep hills above the stream. The impact on the populations of the numerous species of amphibians resident in the environs of the stream is unknown, but is thought to be substantial.

Etymology.—The name *chrysopleura* is derived from the Greek words *chrysos* and *pleura,* meaning "gold" and "side," respectively, in reference to the yellow flash markings on the frog.

Discussion

With the description of *Plectrohyla chrysopleura,* the genus now comprises sixteen described species. The recent reapprasial of the genus by Duellman & Campbell (1992) perforce leaves a number of questions unanswered.

Duellman & Campbell (1992) described two new species of *Plectrohyla* (*P. acanthodes* and *P. teuchestes*), segregating them from the formerly composite *P. guatemalensis.* In addition, they conducted "two levels of phylogenetic analysis" of the fifteen known species. The first analysis involved an attempt to identify suitable out-groups and to establish the monophyly of *Plectrohyla.* The second was an effort to create a cladogram for the in-group, *Plectrohyla.*

As Duellman & Campbell (1992:25) acknowledged, ". . . the morphological data set that [was used] is not sufficent to resolve the phylogenetic relationships among the species of *Plectrohyla.*" Questions also exist concerning their out-group analysis. We discuss our concern with the latter first.

Duellman & Campbell (1992) identified four synapomorphies uniting *Plectrohyla* and the *Hyla bistincta* group as sister-taxa. Unfortunately, they do not unequivocally indicate their concept of the latter group. They make reference to the work of Duellman (1970), who recognized the *Hyla bistincta* group as comprising nine species. They (1992:21) further stated that two of the species included by Duellman (1970) in the group, *H. charadricola* and *H. chryses,* ". . . lack the thick, glandular dorsal skin characteristic of the other, larger species in the group." As a consequence, they did not include these species in the first out-group. No mention was made, however, of the species described and placed subsequently in

the *bistincta* group or related groups by Adler & Dennis (1972) and Caldwell (1974). The latter work is especially important, inasmuch as Caldwell reorganized the members of Duellman's (1970) *bistincta* group (plus the species described subsequently, including her own, as well as *H. arborescandens*) into four species groups (*bistincta, arborescandens, charadricola,* and *crassa*), leaving the *bistincta* group with only two members (*bistincta* and *pentheter*). Perhaps, Duellman & Campbell (1992:21) had Caldwell's study in mind when they penned the quizzical statement, "The monophyly of the *Hyla bistincta* group seems to be assured, but the limits of the group remain to be ascertained." This statement appears to constitute a reverse non sequitur, i.e., the second clause of the sentence is supposed to follow from the first. Group limits (i.e., content) have to be established before a case for monophyly can be made. If this had been done, making a case for the *bistincta* group as the first out-group and sister-taxon of *Plectrohyla* would rest upon a secure base instead of being equivocal.

The choice of the second out-group, the species *Hyla miotympanum,* by Duellman & Campbell (1992:21), was acknowledged to be ". . . frought [sic] with uncertainty." They appear to have selected this taxon by a process of elimination, excluding from consideration various groups of stream-breeding hylines with highly-specialized tadpoles. They doubtless had little choice, inasmuch as their decision was hampered by ". . . the absence of phylogenetic analyses of the diverse groups of hylids" (p. 21). In light of the questions concerning the choice of out-groups, we wonder what weight can be given to the determination of features as apomorphies or plesiomorphies. Pursuing the work to clarify such matters is outside of the scope of the present work and thus we tentatively accept Duellman & Campbell's (1992) out-group analysis in attempting to determine the phylogenetic position of *Plectrohyla chrysopleura.* We also accept the hypothesis that the genus *Plectrohyla* is

Table 2.—Morphological characters and coded character states used in phylogenetic analysis of *Plectrohyla*. Number in parentheses following a character refers to the respective character number in Duellman & Campbell (1992). State 0 is the primitive condition. Character transformation is 0 → 1 in all characters except character 3, which is 0 → 1 → 2 → 3.

Character	Character states
1. Squamosal (11)	0: otic ramus of squamosal articulating with the crista parotica 1: otic ramus of squamosal not articulating with the crista parotica
2. Humerus (12)	0: humerus round in section 1: humerus having well-developed flanges
3. Prepollex (13)	0: prepollex slightly enlarged, cartilaginous or ossified, rounded or elliptical 1: prepollex enlarged, elongated, ossified, flat, terminally blunt 2: prepollex enlarged, elongated, ossified, terminally curved with a single spine 3: prepollex enlarged, elongated, ossified, with two curved spines
4. Rostrum (14)	0: rostrum plain 1: rostrum with vertical keel
5. Linea masculinea (15)	0: linea masculinea absent 1: linea masculinea present
6. Vocal slits (16)	0: vocal slits present 1: vocal slits absent
7. Expansion of oral disc (18)	0: oral disc not expanded and suctorial 1: oral disc expanded and suctorial
8. Serrations on upper jaw sheath (19)	0: serrations subequal in size 1: two or more serrations enlarged, fanglike
9. Length of posterior tooth rows (21)	0: posterior tooth rows shorter than anterior rows 1: posterior tooth rows equal in length to anterior rows
10. Lateral processes on upper jaw sheath (20)	0: lateral processes well-developed 1: lateral processes weak or absent
11. Maxillary teeth	0: maxillary teeth spatulate 1: maxillary teeth pointed

monophyletic, although we feel that such an opinion would stand on much firmer footing were the phylogenetic relationships within the presumed sister-taxon, the *Hyla bistincta* group, and those of Middle American stream-breeding hylids in general, better understood.

The in-group analysis of *Plectrohyla* carried out by Duellman & Campbell (1992), however, is particularly frustrating, in part due to the uncooperative nature of the members of the genus. Sufficient-sized series of some of the species of *Plectrohyla* are notoriously difficult to assemble. Nonetheless, rendering a strict consensus tree possessing a polytomy of 11 clades for 15 spe-

cies is close to having no in-group analysis at all. For Duellman and Campbell to imply in the title that their paper somehow resolves the "phylogenetic relationships" of the species of *Plectrohyla* is certainly misleading.

The characters and states used by Duellman & Campbell (1992) in the in-group analysis contain several mistakes and/or potential ambiguities. We thought that a more effective analysis would modify their hypothesis about the group relationships. As a result, we undertook a phylogenetic reanalysis of the genus *Plectrohyla*; discussion of our treatment of characters follows.

A major oversight of Duellman & Camp-

bell was the fashion in which the states associated with the prepollex were coded in the out-group (their character 8) and ingroup (their character 13) analyses. The enlarged, ossified nature of the prepollex in species of *Plectrohyla* was cited as evidence for the monophyly of the genus. In the ingroup analysis, however, three states were identified for this character, viz., (1) blunt, (2) pointed, simple, and (3) pointed, bifid. The polarization and transformation serialization was identified as $0 \rightarrow 1 \rightarrow 2$ in the same order. The "0" condition, however, was stated by Duellman & Campbell (1992: 23) to be "The primitive condition (that found in both the first and second outgroups) . . . ." Thus, a blunt, enlarged, and ossified prepollex is indicated as occurring in *Hyla miotympanum* and members of the *H. bistincta* group. Such is patently not the case, so the character states and their polarity were recoded (Table 2).

A second concern is with Duellman & Campbell's character 17 (rows of accessory papillae). Two states were given for this character as follows $(0 \rightarrow 1)$:

0 = one row of accessory papillae on each labium.
1 = one row of accessory papillae on anterior labium and two rows on posterior labium.

Five species of *Plectrohyla* (*hartwegi, ixil, matudai, pokomchi,* and *teuchestes*) were said to have the derived state. However, Duellman & Campbell (1984:396) stated that there is a "single row of larger papillae medial to fringing papillae" in *pokomchi.* Their illustration (fig. 6) of the *pokomchi* tadpole also shows one row of large accessory papillae (= submarginal papillae) on the posterior labium in this species. Duellman & Campbell (1992:16) also stated that there are "four or five large submarginal papillae between posterior labial tooth row and posterior margin of lip" in *teuchestes* and (p. 10) that there are "6–8 large papillae medially between third posterior tooth row and posterior edge of disc" in *hartwegi.* Thus,

the situation in *hartwegi* and *teuchestes* is radically different from the condition where there are two rows of submarginal papillae on the posterior labium as found in *ixil* and *matudai* tadpoles (compare illustrations of latter two species in Duellman (1970), with those of *hartwegi* and *teuchestes* in Duellman & Campbell 1992). We have deleted this character from our analysis because of the erroneous scoring of this character by Duellman & Campbell and the fact that an examination of the tadpoles of each species of *Plectrohyla* would be necessary before we could confidently recode this feature. Such an analysis is outside the limits of our study, but we would urge future workers studying the phylogeny of *Plectrohyla* to investigate the potential utility of this character.

A third problem is Duellman & Campbell's character 20 (lateral processes on upper jaw sheath). Three states were given for this character as follows $(0 \rightarrow 1 \rightarrow 2)$:

0 = lateral processes long.
1 = lateral processes short.
2 = lateral processes weak or absent.

Two species (*acanthodes* and *guatemalensis*) were said to have the state 0, two (*avia* and *pokomchi*) state 1, and the remaining species (where known) state 2. Campbell & Kubin (1990:table 1) defined the lateral processes of *acanthodes* (as *guatemalensis*: Campbell & Kubin's source of information for this taxon was Duellman (1970), who actually described and illustrated the *acanthodes* tadpole under the name *guatemalensis*), *avia, pokomchi,* and *sagorum* as "short, narrow." These four species, all with "short" lateral processes, are coded three different ways in Duellman & Campbell's data matrix. Also, numerous contradicting statements can be found in Duellman & Campbell (1992) by comparing the species diagnosis for *acanthodes, dasypus, glandulosa, guatemalensis, pokomchi, quecchi, sagorum,* and *tecunumani* with their data matrix (table 8). Additionally, Honduran *P. glandulosa* tadpoles (*glandulosa* coded state

Table 3.—Character matrix for the species of *Plectrohyla* in the phylogenetic analysis. Missing characters coded 9. Character numbers refer to Table 2.

Taxon	Character										
	1	2	3	4	5	6	7	8	9	10	11
Ancestor	0	0	0	0	0	0	0	0	0	0	0
P. acanthodes	0	1	3	0	0	1	0	0	0	0	0
P. avia	0	1	2	0	0	1	0	0	0	1	1
P. chrysopleura	0	1	1	0	0	0	0	0	0	0	0
P. dasypus	0	1	1	0	0	0	0	0	0	1	0
P. glandulosa A	0	1	1	0	0	1	0	0	0	1	1
P. glandulosa B	0	1	1	0	0	1	0	0	0	0	1
P. guatemalensis	0	1	3	0	0	1	0	0	0	0	0
P. hartwegi	0	1	3	0	0	1	1	0	1	1	0
P. ixil	1	0	2	0	1	0	0	1	0	1	0
P. lacertosa	0	1	1	0	0	1	9	9	9	9	1
P. matudai	1	0	2	0	1	0	0	1	0	1	0
P. pokomchi	0	1	3	0	0	0	0	0	0	1	0
P. pycnochila	0	1	1	0	0	1	9	9	9	9	0
P. quecchi	0	1	2	1	0	0	0	0	0	1	0
P. sagorum	0	1	2	1	0	0	0	0	0	1	1
P. tecunumani	0	1	1	0	0	1	0	0	0	1	1
P. teuchestes	0	1	3	0	0	1	1	0	1	1	0

2 by Duellman & Campbell) have lateral processes similar in length to those of *P. guatemalensis* (*guatemalensis* coded state 0 by Duellman & Campbell). Because of the contradictory evidence, we have recoded this character as either well-developed, or weak or absent (Table 2). This action necessitates distinguishing Guatemalan *P. glandulosa*, with weak or absent lateral processes, from Honduran *P. glandulosa*. These taxa are labeled *glandulosa* A and *glandulosa* B, respectively, in our data matrix (Table 3). The nine species coded in Duellman & Campbell's (1992) data matrix as having "weak or absent" lateral processes were similarly coded in our data matrix, whereas the remaining species (where the tadpoles are known) were coded as well-developed (Table 3).

A final matter relates to the lack of use of a character discussed by Duellman (1970), viz., the nature of the maxillary teeth (spatulate vs. pointed). Maxillary teeth of the *H. bistincta* group (sensu Duellman 1970) are spatulate, as are those of most species of Middle American hylids (Duellman 1970). Thus, we hypothesize that spatulate teeth represent the ancestral state and pointed teeth the derived one. If such were the case (again, what exactly are the limits of the *bistincta* group?), then the character would be polarized and is added to our analysis (Tables 2, 3). Duellman & Campbell (1992) did not indicate condition of the maxillary teeth in *P. acanthodes*, but as specimens of this species were included within the composite *P. guatemalensis* by Duellman (1970), which has spatulate teeth, then those of *acanthodes* probably are spatulate and we have so coded them. The characteristics for all species in the analysis are given in Table 3.

We confined our searches for the most parsimonious phylogenetic hypothesis as closely as possible to the methods used by Duellman & Campbell (1992) in their PAUP analysis. However, our PAUP program (3.0) is a later version than that (2.4) used by Duellman & Campbell. The global branch-swapping option used by Duellman & Campbell is not available on version 3.0; instead a subtree pruning-regrafting (SPR) option is available that is ". . . approximately, but not exactly, equivalent to the
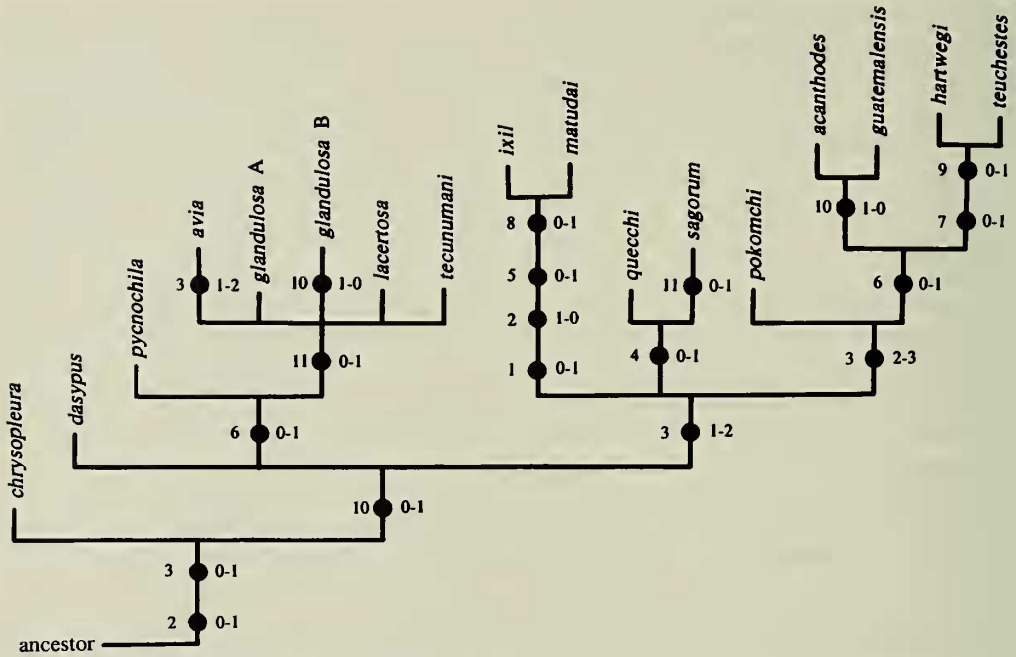
Fig. 3. Strict and Adams consensus cladogram for the members of the genus *Plectrohyla*. Character numbers (to the left of the circles) and changes in character states (to the right of the circles) refer to numbers in Table 2.

'global' procedure used in earlier versions of PAUP" (Swofford, 1991:31 in user's manual). Also available is a new procedure, the tree bisection-reconnection (TBR) option. Also new to PAUP 3.0 is the ability to yield polytomies by collapsing branches having a maximum length of zero. Using the data matrix in Table 3, we made searches using both the SPR and TBR branch-swapping options. Each branch-swapping option was executed first with the zero-length branches collapsed, then executed with the zero-length branches not collapsed. Each search was conducted with the MUL-PARS option in effect, the stepwise addition option closest, and the tree rooted using the outgroup method. Strict consensus and Adams consensus trees were generated for each of the four searches. All eight consensus trees generated were identical, regardless of the search options used. When the zero-length branches were not collapsed, 300 equally parsimonious trees were retained in both the SPR and TBR searches (matrix set at 300, the exact number that can be found is unknown), whereas, when the zero-length branches were collapsed, only two equally parsimonious trees were found under both the SPR and TBR searches. Each of these two trees was identical to its counterpart under the other branch-swapping option. Tree 2 differs from tree 1 (Fig. 3) only by *glandulosa* B + *lacertosa* forming a clade by assigning a reversal to character 10, which is missing datum for *lacertosa*. All trees have 19 steps and a consistency index of 0.684. Thus, even though our data matrix contains an equal number of characters, plus two more taxa than Duellman & Campbell's matrix, our trees are one step shorter and have a slightly higher consistency index (0.650 in Duellman & Campbell's trees). More importantly, the unresolved polytomy of 11 clades for 15 taxa in Duellman & Campbell's strict consensus tree (their fig. 19) is almost fully resolved (Fig. 3). Whereas our cladogram can undoubtably be improved upon by a more thorough analysis

of the genus, it is a substantial improvement over that offered by Duellman & Campbell. *Plectrohyla chrysopleura,* the species herein described, is the species closest to the ancestral stock of the genus, based upon our phylogenetic analysis.

A more minor concern, but nonetheless irritating, with the Duellman & Campbell (1992) revision are contradictions between some tadpole descriptions and their identifying characteristics in the tadpole key or one of the tadpole illustrations. Duellman & Campbell (1992:4) stated that the posterior tooth rows of *acanthodes* tadpoles are ". . . slightly shorter than upper [= anterior] rows, third shortest," whereas, in the key we are told in couplet 7, leading to *acanthodes* in couplet 9, that the posterior tooth rows are subequal in length. The other part of couplet 7, "Third lower [= posterior] labial tooth row shorter than others," leads to couplet 10 and past *acanthodes. Plectrohyla teuchestes* tadpoles supposedly have a "Distinct smooth, sharply raised fold between fringing papillae and anterior tooth row" (Table 3; also see couplet 2 in tadpole key), whereas Duellman & Campbell's drawing of the *teuchestes* tadpole (their fig. 15) indicates that the "fold" is papillate or scalloped throughout. Also, Duellman & Campbell (1992:fig. 8) illustrate the *P. guatemalensis* tadpole with the caudal musculature extending dorsally onto the body nearly to the eyes, quite a remarkable feature. Other statements also are confusing: i.e., *acanthodes* tadpoles with "two rows of small labial papillae fringing disc, except only one row midventrally" (p. 4) or "Lips having a single row of small fringing papillae" (couplet 5 leading to *acanthodes*); and *guatemalensis* tadpoles reported to have "one row of small labial papillae anteriorly and laterally, two rows midventrally" (p. 8) but "Lips having two rows of small fringing papillae" (couplet 5 leading to *guatemalensis*). Considering the extent of the Duellman & Campbell inconsistencies, we suggest that anyone trying to use their tadpole key do so with caution. Finally, the specific name *pycnochila* is misspelled throughout Duellman & Campbell's paper as *pychnochila* and the number in the second section of tadpole couplet 3 leading to couplet 5 is misprinted 6.

Acknowledgments

Literature Cited

Adler, K., & D. M. Dennis. 1972. New tree frogs of the genus *Hyla* from the cloud forests of western Guerrero, México.—Occasional Papers of the Museum of Natural History, The University of Kansas 7:1–19.

Altig, R., & G. F. Johnston. 1986. Major characteristics of free-living anuran tadpoles.—Smithsonian Herpetological Information Service 67:1–75.

Caldwell, J. 1974. A re-evaluation of the *Hyla bistincta* species group, with descriptions of three new species (Anura: Hylidae).—Occasional Papers of the Museum of Natural History, The University of Kansas 28:1–37.

Campbell, J. A., & T. M. Kubin. 1990. A key to the larvae of *Plectrohyla* (Hylidae), with a description of the tadpole presumed to be *Plectrohyla avia.*—The Southwestern Naturalist 35:91–94.

Duellman, W. E. 1970. The hylid frogs of Middle America.—Monograph of the Museum of Natural History, The University of Kansas 1:1–753.

———, & J. A. Campbell. 1984. Two new species of *Plectrohyla* from Guatemala (Anura: Hylidae).—Copeia 1984:390–397.

———, & ———. 1992. Hylid frogs of the genus *Plectrohyla*: systematics and phylogenetic relationships.—Miscellaneous Publications Museum of Zoology, University of Michigan 181:1–32.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification.—Herpetologica 16:183–190.

Holdridge, L. R. 1967. Life zone ecology. Second ed. Tropical Science Center, San José, Costa Rica, 206 pp.

McCranie, J. R., J. M. Savage, & L. D. Wilson. 1989. Description of two new species of the *Eleutherodactylus milesi* group (Amphibia: Anura: Leptodactylidae) from northern Honduras.—Proceedings of the Biological Society of Washington 102:483–490.

———, & L. D. Wilson. 1986. A new species of red-eyed treefrog of the *Hyla uranochroa* group (Anura: Hylidae) from northern Honduras.—Proceedings of the Biological Society of Washington 99:51–55.

———, ———, & K. L. Williams. 1989. A new genus and species of toad (Anura: Bufonidae) with an extraordinary stream-adapted tadpole from northern Honduras.—Occasional Papers of the Museum of Natural History, The University of Kansas 129:1–18.

Myers, C. W., & W. E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama.—American Museum Novitates 2752:1–32.

Savage, J. M., & W. R. Heyer. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America.—Beiträge zur Neotropischen Fauna 5:111–131.

———, J. R. McCranie, & L. D. Wilson. 1988. New upland stream frogs of the *Eleutherodactylus rugulosus* group (Amphibia: Anura: Leptodactylidae) from Honduras. Bulletin of the Southern California Academy of Sciences 87:50–56.

Smithe, F. B. 1975. Naturalist's color guide. The American Museum of Natural History, New York, 182 color swatches.

Stuart, L. C. 1963. A checklist of the herpetofauna of Guatemala.—Miscellaneous Publications Museum of Zoology, University of Michigan 122:1–150.

Swofford, D. L. 1991. PAUP: phylogenetic analysis using parsimony, version 3.0s. Illinois Natural History Survey, Champaign.

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